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ON THE MATING SWARMS OF CERTAIN CHIRONOMIDAE (DIPTERA)

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Communicated by Dr. Llewellyn Lloyd, F.R.E.S.

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In many insects mating is preceded by an aggregation of individuals which indulge in some collective form of activity, such as the well-known mating swarm of bees or the migratory flight of locusts. Such behaviour reaches its highest development in the complex mating dances of certain Diptera, particularly the Tipulidae, Culicidae and Chironomidae. Descriptions of such dances are abundant in entomological literature, but little seems to be known of the physical factors which govern their occurrence or of the purpose served by this mating prelude.

In the present work an attempt has been made to study in detail the swarming of the chironomid *Spaniotoma* (*Limnophyes*) *minima* Meigen, both in the field and the laboratory, with a view of determining the environmental conditions limiting the formation of swarms and the factors controlling their orientation. Contributory, but less complete, observations have been made on other

chironomids, especially *Metriocnemus longitarsus* Goetghebuer, *M. hirticollis* Staeg and *Chironomus dorsalis* Meigen.

The field observations have been made at the Leeds Corporation Sewage Works, Knostrop, where the first three species occur abundantly in the bacteria beds and *Chironomus dorsalis* breeds freely in the adjacent sewage conduits. The life-history of *Spaniotoma minima* and of the two species of *Metriocnemus* and their environmental relationships at the Knostrop sewage works have been fully dealt with by Lloyd (1935, 1937, 1941) and by Lloyd *et al.* (1940). Since the males of *Metriocnemus longitarsus* and *hirticollis* are practically indistinguishable no attempt has been made to differentiate them and references to *Metriocnemus* in this paper will refer to either species or to both.

2. The Natural Swarms.

(a) *Occurrence and location.*

Under favourable weather conditions *S. minima* has been found swarming throughout the year, but mainly from May to October when the fly is most abundant and temperature most favourable. Certain localities of the sewage works are specially resorted to by the flies. Thus swarms are most frequently seen along the low stone walls, about 12 in. in height, bordering the bacteria beds, over paths and grass verges and in certain sunken concrete pits and channels adjacent to the beds. Swarms of *S. minima* as a rule occur close to the ground, especially in exposed situations, such as over the beds, where they normally keep within a foot of the surface, but in depressions they may rise 5 or 6 ft. above the substratum.

Under the artificial conditions of the bacteria beds both species of *Metriocnemus* emerge throughout the year, but their physiological responses indicate that *M. longitarsus* is adapted to colder conditions than *M. hirticollis*. The former has its greatest period of abundance some time in winter and the latter usually in early summer. Correlated with this seasonal preference *M. longitarsus*, though a swarming species, is able to mate in very confined spaces, but not so *M. hirticollis* which must swarm (Lloyd, 1937). Both species favour the same general situations as *S. minima*, but tend to swarm at higher levels, *e.g.* around the top of the Recorder House (a rectangular brick building, 12 ft. high) and particularly gather round the tops of the travelling distributors, which spray sewage on to the bacteria beds. When both species are active the swarms are mixed, for mated couples of both can be taken below an apparently homogeneous swarm. Swarms of *Spaniotoma perennis* Meigen and *Tanytarsus atrofasciatus* Kieffer are more rarely seen, but when they occur they occupy much the same situations as *Metriocnemus*.

C. dorsalis is usually found above the tops of the concrete pits and channels, above or level with the roof of the Recorder House and high over the paths and beds, sometimes as much as 20 ft. above the surface of the latter.

Thus it is seen that *S. minima*, which is the smallest fly, swarms at the lowest levels whereas the large *C. dorsalis* is found at the highest. *Metriocnemus*, *S. perennis* and *T. atrofasciatus*, which are intermediate in size, frequent the middle levels. This is in agreement with the observations of Harnisch (Gruhl, 1924), who states that among the Chironomidae the smallest species generally swarm close to the earth whilst the largest dance over high points, such as tree-tops, up to 30 m. Edwards (1929) notes a similar disparity in the levels of swarming between different species of Tanypodinae.

The favouring of different levels according to size is excellently shown in the stratification of swarms composed of two or more species, such as are frequently seen at Knostrop. In one such swarm, in a sunken channel, sweeps made with a small net at intervals of 1 ft. above the channel bottom showed that from 0 to 4 ft. the swarm was composed of *S. minima* only, at 5 ft. *S. minima* and *Metriocnemus*, from 6 to 7 ft. *Metriocnemus* only, and from 8 to 10 ft. *C. dorsalis*. Ll. Lloyd (personal communication) has observed a similar swarm in which *T. atrofasciatus* intervened between *S. minima* and *C. dorsalis*. On two subsequent occasions sweeps were made through swarms consisting of *Metriocnemus* and *S. minima* only, occurring in a sunken channel. Ten sweeps were made at each level and the catches for both species were as follows :—

Date	Height, ft.	*S. minima*	*Metriocnemus*
17.v.1941	3	204	0
	5	15	5
	7	6	112
6.vi.1941	2	96	11
	4	84	2
	6	38	19
	7	11	47

The swarming of the smaller flies at the lower levels is probably related to wind. Wind velocity is generally least near the ground and increases rapidly with increasing altitude. If, as one would expect, the larger, more strongly flying species are able to endure greater wind pressures, they will be able to swarm at a higher altitude than the smaller species. This view is supported by the observation of Cambournac and Hill (1940), who state that when swarms of *Anopheles maculipennis* are exposed to a strong breeze the whole swarm sinks closer to the ground.

(b) *Abundance of flies in the swarm.*

The great number of flies often seen dancing at one time is so striking a feature of chironomid swarms that it has frequently been commented on by observers (Howard, Dyer and Knab, 1912, Marshall, 1938). This abundance is particularly exemplified by *S. minima* which, on bright, calm days in summer and early autumn, frequently forms enormous swarms in every part of the sewage works. Single swarms stretch along the end walls of all the terraces of filter beds (40 yd.), the walls bordering the channels (150 yd.) and over the surface of all the beds (36 acres) to a height of about a foot. The numbers of flies in such extensive swarms amount to hundreds of millions.

It is clearly pressure of numbers that causes a lack of orientation in *S. minima* swarms under such conditions, for when the flies are less abundant the swarms are more discrete and at chosen spots whilst, when they are scarce, two or three individuals may be seen dancing over a single blade of grass and in the laboratory, during daylight, a lone fly nearly always chooses the same exact spot for dancing. The other chironomids (*Metriocnemus* spp. and *C. dorsalis*) never achieve an equivalent abundance at the sewage works and so their swarms always remain discrete, more or less spherical, linear or columnar and generally aggregated over some prominent object.

(c) *Fly movement in the swarm.*

Gruhl (1924) has analysed the complex movements of the mating dances of chironomids and has emphasised that they are closely bound up with the necessity for circumventing wind currents. This is achieved by three main methods. In the first, the flight consists of straight lines, separated by sharp angles. Such a flight never takes the insect far from its starting-point. In the second, the insect crosses the air current by oblique lateral movements, as a boatman crosses a stream, whilst, in the third, the insect goes directly against the current so that its own speed cancels that of the wind and the insect appears to float in one place. These three methods are suited to increasing wind velocities —the first to calms, the second to moderate breezes, whilst the third enables a constant position to be maintained against a relatively strong current, but causes the insect to advance whenever the wind backs.

Gruhl's observations have shown the dances of chironomids to be of a very variable structure and to include oblique cruising across the current, vertical movement and direct flight against the wind with retirement whenever the breeze suddenly increases, followed by further advance by means of swifter flight, as in culicines. The present author's own observations show that the dances of the Knostrop chironomids conform to these general principles.

The movements in a mixed swarm of *S. minima* and *Metriocnemus* were studied by placing a sheet of white paper on the bottom of a dry, concrete channel, in which the flies were swarming, and observing the dance from above. The individual flies all faced the breeze and each performed a few, weaving, figure-of-eight movements, hovering against the wind for 1–3 seconds, and then darting off in a straight line for a distance of a few inches. The sequence of movements would then be repeated in the new position. The weaving movements are presumably the retirement and advance in the wind described by Gruhl coupled with a certain amount of vertical movement, whilst the sudden, straight flight is the oblique cruising across the wind front. This flight is not always horizontal, but may contain a small vertical component. The length of the straight flight in *Metriocnemus* was ascertained to vary from 6 to 12 in., while that in *S. minima* varied from 2 to 8 in. The movements of *C. dorsalis* are similar, but the straight flights are more consistently backwards and forwards and less frequently sideways. They vary in distance from 6 in. to 2 ft.

In a closed insectary the lateral flights in *S. minima* swarms are not much in evidence, even when an air current from an electric fan is passed through the cage, the flies hovering steadily against the wind. The wind in this case differs from a natural breeze in being a steady current and, since it is likely that the lateral flight is an adjustment to compensate for variations in the wind force, such flight is unnecessary in the insectary. For the same reason the advancing and retiring movements are not exhibited in laboratory swarms, unless the wind velocity is deliberately varied.

In addition to the individual movements of the flies the whole swarm is subject to sudden surging movements in response to the wind. A sudden gust may drive a whole swarm of *S. minima* backwards for a distance of 1 to 2 ft., the flies advancing again as soon as the wind drops.

(d) *Sex ratio in the swarm.*

It is well known that in most Diptera the swarms are composed almost entirely of males. This has been noted for *Culex pipiens* by Knab (Howard, Dyar and Knab, 1912) and for *Chironomus* by Taylor (Miall and Hammond, 1900), who observed, however, that when swarming was disturbed by wind the

percentage of females is raised, since copulation is hindered and the females remain longer in association with the males.

A similar disproportion in the sex ratio has been found among the Knostrop chironomids. Sweeps through swarms of *S. minima* and *Metriocnemus* gave 7 per cent. of females in the former (1654 m., 116 f.) and 1·3 per cent. (752 m., 10 f.) in the latter. In sweeps through a single swarm of *C. dorsalis* 129 males were captured and no females.

Gruhl (1924) tentatively suggested that the disproportionate sex ratio found in swarms of flies may reflect a similar disproportion in the actual fly population, the more abundant sex forming the swarm whilst the less numerous seeks it. This view is not of universal application and in many cases the apparent disproportion between the sexes may be due to a difference in habit. In *S. minima* and *Metriocnemus*, where the proportion of females in the swarm is always very low, the natural sex ratio of the flies, whether bred in culture from the eggs or captured from the bacteria beds in traps, is found to be equal.

Similarly, Gruhl quotes cases among the culicines where only the males swarm, but the females are equal or greater in actual abundance and from these considerations he concludes that the decisive factor is not so much the absolute proportion of the sexes, but the time at which they emerge—the more numerous sex usually emerging first. An extreme instance is afforded by *Aporomyia dubia* where the males swarm early in May and are seldom seen later, whereas the females first appear at the end of May.

Trapping records show equality of sex in *S. minima* and *Metriocnemus* throughout the year. In *S. minima*, at least, the females are capable of performing the dance in exactly the same manner as the males, for in insectary swarms, where only a few flies are present, males and females are seen to take part in the dance in equal numbers but, when the swarm is large, males form the vast majority. The reason for this becomes apparent when a trap of *S. minima* is opened in the insectary under the appropriate conditions for swarming (see p. 269). A large proportion of the flies, both males and females, rise out of the trap and hover violently near the top of the cage, while others come to rest on the sides, roof and floor. No real dance is performed for the first minute or so, for most of the males are busily engaged in pairing with the females and the mated couples fall thickly on to the bottom of the cage. Soon, however, a dance is established consisting mainly of males. The reason for this is that the females, once mated, do not rise again into the swarm, but remain resting on the floor of the cage, whereas the males usually rejoin the dance as soon as copulation is completed. Thus the proportion of females in the swarm steadily falls until no further copulations occur, which condition is usually reached after 20–30 mins. In natural swarms, where the supply of females is virtually unlimited, pairing does not cease as long as the environmental conditions remain suitable for mating, but the number of females present in the swarm must necessarily be much less than the number of males. After the first rush of matings in the laboratory cage females may be seen to rise at intervals and enter the swarm, where, if the latter is large and vigorous, they are speedily seized by males and drop to the floor *in copulo*. In the field the same behaviour has been observed, but owing to the greater size of the swarms, the females never penetrate far before they are caught.

(e) *Copulation.*

The process of copulation has been studied both in field and in laboratory dances of *S. minima* and resembles that described by Knab (Howard, Dyar and Knab, 1912) for *Culex pipiens*. The females lurk beneath the swarm, resting

on the floor and sides of the channels, on walls, blades of grass, stones, etc. From time to time individual females leave their resting-places and fly upwards into the swarm. In the mating cage, where fewer flies are involved, the females may perform dancing movements for some time before they copulate, but in natural swarms they are usually seized immediately by a male. The actual process of pairing is not clear as the two flies whirl rapidly round each other for a fraction of a second and then, united, drop to the ground. Generally they appear merely to allow themselves to fall out of the swarm, rather than fly from it, but where couples appear on the sides of the insectary, or of a channel or pit, some flying has probably taken place. The flies usually alight on their sides, ventral surfaces opposed, and facing in the same direction. A short struggle then ensues until they right themselves. The final position is tail to tail. The couple may remain still or walk about, the stronger female invariably pulling. Copulation in *Metriocnemus* and *C. dorsalis* is essentially similar.

In the above species the final position is always tail to tail. In mosquitoes the final position depends on the nature of the claws in the female (Howard, Dyar and Knab, 1912). If these are simple the flies copulate " unwound " (*i.e.*, tail to tail), if toothed, with the ventral sides opposed. *S. minima* also obeys this rule, for the female claws are simple and copulation is tail to tail.

The time which elapses between the alighting of a pair and their subsequent parting is very variable. In *S. minima* variations from almost instantaneous parting to copulations of as long as 10 mins. have been observed, the average being 1–3 mins. It is not known whether the very transitory copulations result in equal fertility with the lengthier matings. It is likely that the immediate break up of a pair on alighting is due to the male failing to obtain a proper grip on the female genitalia and the mating would therefore be sterile.

As mentioned above, the frequency of copulation in a laboratory swarm is at first very high, but soon declines and after 20 mins. or so has fallen almost to zero. In a natural swarm it varies greatly with the size and activity of the dance. Thus, from a swarm of *Metriocnemus* over a grass bank, only one couple alighted on a sheet of white paper below the swarm during the first 10 mins. of observation. Suddenly (coinciding with a drop in the wind) there was a great increase in the size and activity of the swarm and the characteristic high-pitched hum of a vigorous dance was heard. Mating couples then dropped rapidly on to the paper, 10 being seen in the first minute. In an active *S. minima* swarm in one of the concrete channels 34 pairs were captured on a sheet of white paper in 45 minutes, but since the sheet was not large enough to underlie more than half the swarm, and a large number of mating couples escaped capture, the actual number of matings was considerably in excess of this figure.

An attempt has been made to assess the degree of fertility resulting from the matings. Mating pairs were captured from the ground in small glass tubes, closed with corks nicked and plugged with cotton wool, to allow free entry of the air. In the laboratory a little of the effluent from the bacteria beds was added to enable the females to oviposit. The tubes were kept at laboratory temperatures and examined daily until oviposition took place, when the eggs were counted. The parent flies were removed and the eggs inspected daily until they hatched and the number of infertile eggs was noted. 365 pairs, from 14 different swarms, were tested and 63% of the females captured laid batches containing fertile eggs. Since the flies which parted immediately on alighting were not captured, only copulations of some duration were counted.

3. Production of Mating Swarms in the Laboratory.

(a) *Introduction.*

The various species of swarming Diptera differ in their ability to mate in small cages in the laboratory. Those which are able to mate in confinement are termed stenogamous and those unable to do so eurygamous. The root of the inhibition seems to lie in the inability of the flies to form the mating dance under the artificial conditions imposed by an insectary, for *Anopheles maculipennis* var. *atroparvus*, which can dispense with the swarm, will breed freely in small vessels, whilst most other subspecies of *A. maculipennis*, which are unable to mate without swarming, cannot breed in close confinement. In part the difficulty results from the fact that the small cage gives insufficient space for the formation of a dance. Thus the males of *A. maculipennis* var. *atroparvus* are unable to swarm in small vessels, but can do so in an insectary 14 × 8 × 7 ft. (Marshall, 1938), whilst *typicus* has been made to swarm in a large cage, 26 × $12\frac{1}{2}$ × $15\frac{1}{2}$ ft., but not in one of 15 cu. ft. capacity (Hackett and Bates, 1936). The latter authors also record that *superpictus*, *elutus* and *bifurcatus*, which cannot swarm in small cages, dance freely in a room $6\frac{1}{4}$ × $5\frac{3}{4}$ × $6\frac{1}{2}$ ft. Cambournac and Hill (1940) regularly observed swarms of *A. annularis* in barns and stables, whilst Gruhl (1924), and Rao and Russel (1938), have noted dances of species of *Culex* in houses. *S. minima* and *Metriocnemus* will also swarm if freely released into the laboratory, usually choosing certain specially favoured positions.

The relation between the volume of the chamber and the size of the fly (and, therefore, the amplitude of its dancing movements) would also seem to be important in determining whether or not a species will swarm in confinement. Thus, under suitable conditions, *S. minima* will dance vigorously in a cage of approximately 2 cu. ft. capacity and also in much smaller vessels. The larger *C. dorsalis* has never been seen to do so and *Metriocnemus* only rarely, and then only one or two flies at a time.

It would also appear that illumination of the chamber influences the behaviour of the flies, for Bates and Hackett (1939) record that *A. maculipennis* var. *sacharovi* will readily form a swarm directly orientated over a man's head in a small room when the latter is illuminated from the ceiling with a dim light, whilst *labranchiae* will swarm freely in a small cage (39·4 in. high and 19·7 in. wide) if a blue light of about 3 f.c. intensity at a distance of 1·2 in. is placed on top of the cage. The authors were able to maintain a *labranchiae* colony for over a year using this method.

(b) *Mating in* Spaniotoma minima *without a swarm.*

Hitherto *S. minima* has always been regarded as an eurygamous species. Lloyd *et al.* (1940) state that after numerous attempts with flies bred from culture only one effective mating was obtained. J. R. Welch (unpublished) also failed, using a variety of methods. It was, however, noted (Lloyd *et al.*, 1940) that when a trap-full of wild flies was released into a small bell-jar, close to a window, a few copulations occurred in the first rush of flies out of the trap, as they struggled in a heap on the lighter side of the jar, but thereafter no more matings took place, however long they were kept.

An attempt was therefore made to induce mating merely by stimulating the flies to activity. Several hundred flies, freshly trapped from the bacteria beds, were released into an elongated glass vessel made by connecting two bell-jars

(each 8 × 5 in.) mouth to mouth. The vessel was placed horizontally on a bench with the apex of one jar pointing towards a window. *S. minima* is strongly phototropic and the released flies immediately crowded to the end nearer the light and a number of mating couples resulted from the initial rush from the trap. The vessel was periodically reversed so that the flies alternately migrated from one end to the other and a few more mating couples were observed. The mated females, however, did not join in the movement, but remained resting on the glass at the darker end. These females were removed for a fertility test. At the end of the experiment these, together with 30 representative unmated females from the light end, were set up in small tubes containing a little water for oviposition. Of a total of 74 females tested only 35 (47%) oviposited and of these only two laid fertile eggs. Thus, although the experiment is inconclusive, it corroborates Lloyd's conclusion that when males and females of *S. minima* are stimulated to activity, although some mating results, only a very low rate of fertility is to be expected. Moreover, since the flies used were captured from the beds, the two females which laid fertile eggs may well have been fecundated prior to the experiment.

(c) *Production of the mating dance in confinement.*

From the foregoing experiences it seemed that the formation of the nuptial dance was a necessary prelude to successful mating and preliminary experiments suggested that light was of fundamental importance.

In order to investigate the effect of illumination a special insectary was constructed, having a wooden framework 20 × 10 × 12½ in. supported on two wooden battens each 1¾ in. deep. The sides and ends of the cage were formed by glass plates sliding in the wooden framework, so that they could be removed and replaced by sheets of bolting silk for other experiments. The top was covered with bolting silk and the floor was formed by a sheet of glazed, white cardboard, replaceable by a sheet of glass when required.

In each of a series of tests a trap containing two or three hundred wild flies was opened in the cage in a darkened room. When exposed to the light of a single 40-watt lamp, shining on one end of the cage, most of the flies crowded towards the illuminated end and settled on the glass, while others remained at rest on the roof, floor and sides. No mating swarm was formed, although occasionally two or three flies would perform intermittent dancing movements at the dark end of the cage. When the front or back of the insectary was illuminated by a single lamp a similar result was observed, the flies settling on the illuminated side, but the tendency to intermittent dancing was rather more marked. With any two sides illuminated simultaneously, each by a single lamp, a small swarm usually formed in the middle of the cage and, when all four sides were illuminated, a larger swarm resulted. A vigorous dance, however, could be produced only with vertical illumination, either from above or below. The swarm was most vigorous when the illumination was from above and usually kept within two or three inches of the top of the cage, whilst, with lighting from below, it formed close to the floor.

These results indicate that even lighting is essential for the production of the mating swarm and explains why dancing does not occur in a glass bell-jar in front of a window. With unidirectional illumination in a horizontal plane the positively phototropic flies gather in front of the source of light and the free-flying movements necessary for the dance are inhibited. As the horizontal lighting becomes more and more even, by the use of two or four lights from

different directions, the dancing response grows more marked. It seems to be fully stimulated only when either the dorsal or ventral ommatidia of the eyes receive most of the light, especially in the former case, for it is from above that most of the light strikes the eye in a natural swarm.

For the regular production of laboratory swarms for experimental purposes and the maintenance of laboratory culture of larvae the insectary described above was used, the two glass ends being replaced by sheets of bolting silk fastened to the framework of the cage, the bottom half of each being left unfastened so that the hands could be inserted for the removal of mating couples and the manipulation of apparatus. A white cardboard floor was used and illumination provided by two 40-watt pearl lamps suspended 4 in. above the cage. Two lamps were used in preference to one, since they gave a stronger and more even illumination, which resulted in a larger swarm. Since lateral light had to be eliminated, the experiments were always performed in a darkened room. The wild flies used were trapped from the bacteria beds and each trap contained from 50 to 3000 flies according to the time of year. The behaviour of the flies has already been described (p. 269). The dance, which often included several hundred individuals, differed little in character from the natural swarms except that, as the air was still, the flies faced in all directions (see p. 270). From time to time the females were seen to leave their resting-places and enter the dance, while mating couples fell from the swarm on to the floor. In vigorous dances mating is at first so abundant that 50 or more couples have often been seen on the floor at one time. The duration of copulation is similar to that in natural swarms. Not all the flies emerge from the trap and some of those emerging appear to take no part in the swarm.

There seems to be a relationship between the number of flies present and the activity of swarming. Although individual flies may dance actively, particularly when free in the laboratory (*e.g.*, under a suspended lamp), a small catch usually produces a sluggish swarm, or sometimes no swarm at all, whilst a large catch invariably results in an active dance with abundant mating. It is likely that mass stimulation plays some part.

The fertility of laboratory matings of wild flies was determined in a similar manner to that used for natural swarms. Of 203 pairs tested, 114 females laid fertile eggs, giving a total percentage fertility of 56, or 7% less than that for natural dances.

In an attempt to produce similar results with laboratory-bred *S. minima*, flies were bred in bulk in glass jars containing a large number of egg batches on a culture medium of bed alga on a substratum of damp cotton wool (Lloyd, *et al.*, 1937). The jars were kept corked for some days between the experiments until a sufficiently large number of flies had accumulated. The conditions for swarming were exactly the same as those used for the wild flies, but the laboratory-bred insects were more sluggish and swarmed less readily, and it was frequently necessary to stimulate dancing by tapping the side of the cage. This was probably due in part to the smaller number of flies involved (100–200 in each experiment). From 64 pairs captured for fertility tests 27 fertile oviposition resulted, giving a percentage fertility of 42, which is somewhat less than that obtained from wild flies, either in the laboratory or from natural swarms.

Thus, under the conditions described, it was possible to produce successful insectary swarms of *S. minima* both with wild and with laboratory-bred flies, and, in spite of the tendency to sluggishness in the latter, a supply of fertile eggs could be obtained.

4. The Effect of Climatic Conditions.

(a) *Wind.*

It is well known that the mating dance in Diptera is profoundly affected by meteorological conditions and clearly, since small insects are unable to maintain themselves in the air against strong currents, wind is of prime importance.

i. Effect on the occurrence and position of swarms.

Many authors have recorded that anophelines, culicines and chironomids swarm on the lee of sheltering objects in windy weather and that on days of high-wind velocity swarming ceases entirely. Observations at Knostrop confirm these statements. The prevailing wind force was measured with a Dine's anemometer 16 ft. above the ground. With a force of 10 m.p.h. or less and other conditions favourable, swarming was so general over the beds and channels that one would have judged that the flies were not seeking shelter; but with a wind force prevailing at 20 m.p.h. swarming was clearly restricted to the most sheltered sites. Tests made in the swarms at the lower velocity showed, however, that the prevailing force gave no idea of the relative calm in which the flies were actually swarming, a remarkable degree of shelter being given simply by proximity to the bed surface, the grass or, at higher levels, a wall or building.

ii. Limiting wind velocity.

Few authors appear to have made any quantitative estimation of the effects of wind on swarming. Rao and Russel (1938) measured velocities in swarms of *Anopheles annularis* and *Culex* sp. and record dancing in winds as strong as 220 ft./min. (2·5 m.p.h.). On a perfectly calm night no swarming was observed and the authors suggest that this may indicate that a certain amount of wind is necessary for swarming. While possibly correct for *A. annularis*, this view cannot be of general application, for several species of Diptera will swarm in insectaries in the complete absence of wind and *S. minima* has been made to dance in a closed cylinder in which all possibility of air currents, even of convection currents, had been excluded (p. 287).

The maximum wind velocity in which the aphid *Myzus persicae* is willing to fly has been determined by releasing the insects into a glass cylinder through which an air current of known velocity was passed (Davies, 1936). A somewhat similar method has been adopted here to investigate the limits of wind endurance of *S. minima* swarms.

The mating cage was used as a wind tunnel. The floor was a sheet of white cardboard, the two ends were covered with fine-mesh bolting silk and the remaining walls were formed by glass plates. The illumination was constant throughout the experiments and was provided by two 40-watt pearl lamps suspended above the cage, the room being otherwise in darkness. An electric fan opposite one end of the cage furnished the source of wind. The wind velocity inside the cage was controlled (*a*) by varying the speed of the fan through a rheostat and (*b*) by varying the distance from the fan to the cage. The wind velocity was determined inside the cage by means of a Biram anemometer supported in the region where swarming is usually most vigorous. The velocity, thus measured within the swarm itself, was that actually experienced by the dancing flies. The Biram anemometer was not sensitive to velocities below 60 ft./min. (0·68 m.p.h. approx.) and for lower speeds an Ower's anemo-

meter was used. The working parts of this instrument are exposed and consequently it was not possible to use it in the swarm as flies would clog the mechanism. Velocities were, therefore, determined beforehand and the conditions reproduced when the anemometer had been removed and the flies released into the cage. Such readings will, however, be subject to error and must be regarded as approximate. A trap of wild flies was then opened in the cage and as soon as the swarm was well established the fan was switched on, the wind velocity in the swarm measured (unless determined previously, as with the Ower's anemometer) and the behaviour of the flies noted. The fan was then switched off and the swarm allowed to recover. Two more observations were made at each wind velocity. The fan was next adjusted to a new speed and the process repeated over the whole range of velocities used. The entire experiment was performed three times with different catches of flies from the beds.

The results of these experiments showed that up to about 50 ft./min. (0·57 m.p.h.) the breeze had scarcely any effect on the swarms except that the flies, which had been previously hovering with their heads pointing in all directions, now turned to face the oncoming wind. Sometimes the flies were blown back an inch or two from the end of the cage nearest the fan, where the wind velocity was highest, but the swarms persisted undiminished. Above this point the swarms were progressively reduced in size with increasing wind velocity, flies dropping out of the dance, one by one, as though exhausted with the effort of contending against the wind. Up to about 100 ft./min. the flies could be made to take to flight by tapping the substratum on which they were resting, but they settled again in a few seconds and showed no inclination to swarm. Above this velocity it was not found possible to induce flight by any means. Above 200 ft./min. (2·27 m.p.h.) swarming ceased almost instantaneously. The whole swarm was blown backwards by the wind and the flies settled immediately on the walls of the cage.

It must be emphasised that none of these critical points is clearly defined. Flies from different catches differ in vigour and, except at the highest velocities, a swarm is dispersed only gradually. Moreover, if one batch of flies is exposed to the same wind force on two consecutive occasions, the swarm may be dispersed instantaneously on one occasion whilst, on the other, a few individuals may persist in dancing for as long as two or three minutes. It is therefore impossible to determine exactly where each end point lies and the above figures are only approximate.

Measurements with the Biram anemometer have also been made in field swarms of *S. minima* and *Metriocnemus* (the anemometer being held in the densest part of the swarm) and compared with the velocity in regions where dances were absent. The observations showed vigorous swarming of *S. minima* taking place in velocities up to 90 ft./min. This is considerably higher than the equivalent point determined for laboratory swarms (about 50 ft./min.), but the outdoor swarms are subjected to gusty winds which never blow with the same force for more than a few seconds together and consequently there are periods of lower velocity in which a disturbed swarm can recover, whereas the laboratory swarms in the wind tunnel are exposed to currents of constant velocity, allowing no periods of recovery. From 100 to 160 ft./min. reduced swarms have been recorded, whilst no *S. minima* swarm has been seen to maintain itself in velocities of over 200 ft./min. (2·27 m.p.h.).

In *Metriocnemus* reduction of the swarm begins at the same velocity as in *S. minima*, but dancing has been observed in velocities as high as 280 ft./min. (3·18 m.p.h.).

On certain occasions swarms have been seen to be dispersed by winds well below the threshold velocity. Thus a swarm of *S. minima* in one of the channels was put down by gusts measured as 100 and 110 ft./min., but on this occasion, although weather conditions were favourable, the trap catches from the bed were low and it seemed likely that a low population level had reduced the swarming potential of the flies.

(b) *Light.*

i. Introduction.

It is well known that certain anopheline and culicine mosquitoes dance only at twilight and certain workers have shown that the time of swarming is mainly determined by light intensity in the habitat. In some cases the range of light intensity in which swarming can occur is very narrow and sharply defined. Thus Rao and Russel (1938) in India found that *Anopheles annularis* usually commenced swarming when the light intensity had fallen to between 1·6 and 1·9 foot-candles and continued until the intensity was too low to measure. Owing to the rapid onset of darkness in that latitude, swarming was thus restricted to a period of 10 mins. in each evening. Cambournac and Hill (1940) found wider limits of toleration for *A. maculipennis* var. *atroparvus*—swarming out of doors usually beginning when the light had fallen to 35–40 f.c., the dances being at their maximum between 2 and 0·02 f.c. and dispersing less than 10 mins. later when the light intensity was too low to measure. Swarms inside buildings commenced at lower intensities than those outside and swarms in different buildings differed markedly in their upper limits of light toleration.

Since the same light intensities recur as the sun rises it is reasonable to suppose that swarming would again take place at dawn. Both pairs of workers have made observations, but in neither case was matutinal swarming seen, although Cambournac and Hill record a daily migration of mosquitoes away from light into the shelter of buildings, etc., commencing when the light intensity reached 6 f.c. and completed by the time it was 45–50 f.c.

ii. Field observations.

Measurements of light intensity, both in field and laboratory swarms, have been made with a Weston no. E. 703 photometer which measures intensities from 0 to 50 f.c. By means of a mask provided with the instrument the range can be extended to 500 f.c. and a second mask was specially made to increase the range to 15,000 f.c. These higher readings are of course subject to considerable error and it now seems likely that all the readings above 500 f.c. are too low. All measurements of general daylight were made with the photometer resting on the same region of one of the bed walls with the target pointing directly to the sky, so that all the readings were strictly comparable. Other readings were taken in the centres of the swarms with the target pointing upwards and so represent the average intensity of direct light falling on the flies.

The light behaviour of the chironomids studied falls into two classes. The swarming of *C. dorsalis* is commonly restricted to short periods after dawn and the evening dusk, with sharply circumscribed limits of light toleration, but *Metriocnemus* and *S. minima* swarm through the day and have been recorded in light intensities of from 500 f.c. (very dull) to over 9000 f.c. (very bright sunlight). Therefore, in order to delimit the effective light range, visits were paid to the works on four occasions at or before dawn.

From these observations it was apparent that the diurnal swarming flies, *S. minima* and *Metriocnemus*, were already dancing long before dawn when the light intensity was only a fraction of a foot-candle and before individual flies could be distinguished. As the light increased, so the swarms became larger and more vigorous and appeared in more situations around the works. In view of the laboratory experiments described below it is improbable that swarming continues during dark nights, but it is not known whether it occurs in moonlight.

The crepuscular swarming *C. dorsalis* was not active during the darkest periods of observation (although even then the outlines of objects could be clearly made out), but began dancing before the photometer registered any light. The swarms, which ranged from 6 to 10 ft. above the bed surface, grew in size and vigour with increasing illumination and reached their maximum between 10 and 30 f.c. As the light became stronger the swarms gradually diminished in size and at the same time sank down into the pits and channels away from the light. Swarming ceased around 120 f.c., but stragglers continued to dance in much higher intensities and small swarms are sometimes seen in broad daylight.

Fly swarming at the Knostrop sewage works reached an abundance at dawn that is unusual during full daylight. The dawn visits were all made on days of favourable temperature and relatively light wind. It is, however, well known that dawn is in general the calmest period of the twenty-four hours and, in spite of the low light intensities then prevailing, it seems to be an exceptionally favourable time for the swarming of even light-loving species. It is possible that during stormy seasons the Knostrop CHIRONOMIDAE may depend largely for their maintenance on the mating which can be performed in the hour or two before and after sunrise.

iii. Laboratory experiments.

As field observations showed that certain of the Knostrop midges are able to perform the mating dance in very low light intensities, laboratory experiments were made with *S. minima* to determine critically the lower limit of illumination for the swarming of this species.

The experiments were performed in a dark room with the mating cage illuminated from above by a 40-watt lamp, low light intensities being obtained by interposing varied numbers of pieces of bolting silk, and intensities below what the photometer would record with accuracy (0·3 f.c.) being estimated in relation to the number of pieces used. Flies trapped from the beds were employed in the four tests made. In three experiments the light intensity was reduced by stages from a maximum value of 20 f.c. (in which swarming is vigorous) and at each stage the behaviour of the swarm was noted but, as in the experiments on wind velocity, it was not found possible to obtain any true quantitative estimate of the amount of swarming at any particular light intensity. In addition to flight, mating resulting from the dance was taken as an additional index of swarming activity.

The first three experiments showed that from 50 to 15 f.c. swarming was vigorous and mating abundant. From 10 f.c. the size of the swarm and the rate of mating became progressively less as the light intensity was reduced, the activity of the flies becoming confined to the top 1–2 in. of the cage (*i.e.*, to the region of highest light intensity). By 0·7 f.c. the swarms were greatly reduced in size and activity, being at the most only one-third of their original size. As the light intensity decreased so more and more flies fell out of the swarm and settled on the roof and sides of the cage, whilst the movements of the insects left in the air showed less and less of the typical dance character, and became

increasingly restricted to mere hovering against the roof and were intermittent with long periods of rest. Mating became less frequent. At 0·005 f.c. (9 thicknesses of bolting silk interposed) the flies were very difficult to see, although it was still possible to distinguish mating couples on the bottom of the cage. At lower intensities most of the flies were at rest or crawling actively on the roof and sides, but from time to time individuals would leave their stations and fly for a few seconds in a straight line before coming to rest on some other part of the cage. At the lowest intensities of all (up to 16 thicknesses of bolting silk) it was impossible to distinguish the flies in the air, but an intermittent hum showed that some flying must still have been in progress. Mating was then very infrequent, but couples were seen even at the lowest intensities.

The decline in the mating at the lower light intensities might have been, wholly or partly, an expression of the normal fall due to the exhaustion of the supply of available females and not of the reduction of illumination. At the end of Exp. 2, therefore, the process was reversed and the light was raised from the lowest intensity when, with 16 thicknesses of bolting silk interposed, the flies were practically all at rest and only two mating couples had been seen in 5 minutes. Fly activity immediately increased and at the intensity of 20 f.c. a very vigorous, deep swarm was in progress and abundant mating resulted. Similarly, at the end of Exp. 3 the light was raised from the same minimum value successively to 0·02, 2 and 22 f.c. Swarming rapidly increased as before but the matings during a 5-minute period at each stage were 3, 1 and 0 respectively. In this case it would appear that the females were already exhausted by the earlier, very vigorous swarming.

In Exp. 4 the light was gradually raised from the lowest intensity to the highest, except that, on releasing the flies, they were exposed for a few minutes to an illumination of 20 f.c. to stimulate their emergence from the trapping jar and it was observed that the mating rate was rather lower than usual at that intensity. With 16 thicknesses of bolting silk between the lamp and the cage no mating couples appeared in a 5-min. period. It was too dark to see the flies in the air, but sound showed that more or less continuous flying was in progress. No mating occurred with either 15 or 14 thicknesses, although with the latter a somewhat greater volume of sound seemed to indicate increased activity. At this point the insects were suddenly exposed to an intensity of 2 f.c. for a few seconds and, almost immediately, three couples appeared on the floor of the cage. This suggests that swarming and mating could take place, but that the low-light intensities inhibited it. From 13 to 9 thicknesses (0·005 f.c.) no mating occurred although there was a considerable amount of sporadic flying. Swarming was first seen at 0·02 f.c. and mating at 0·08 f.c. (2 couples in 5 mins.) and was vigorous at 20 f.c. The mating rate remained low throughout the experiment.

The laboratory experiments thus corroborate the field observations in showing that swarming and mating in *S. minima* can take place at very low light intensities but that the size and vigour of the swarms become progressively less as the illumination is reduced (at least below 10 f.c.), although the occurrence of mating couples at the lowest intensities used showed that some swarming must be taking place.

Although swarming is reduced at low light intensities the twilight period before dawn is at Knostrop a time of great *S. minima* activity. The explanation is probably twofold –(*a*) the natural environment is more favourable for swarming than the cage and the supply of flies is virtually unlimited, (*b*) the light intensities during the periods of field observation, although too low to

determine with the photometer, were never so subdued as the lowest produced in the laboratory. That low light intensity (*i.e.*, below 10 f.c.) greatly reduces swarming in the field is shown by the increase in the size and vigour of the *S. minima* swarms as the day becomes lighter.

iv. Interrelation of light and wind.

From the foregoing observations it is seen that swarms of *S. minima* and *Metriocnemus* can tolerate a wide range of light intensity but are greatly affected by small changes in the velocity of the wind. It follows, therefore, that during the hours of daylight, wind is usually the limiting factor. Thus, swarming is often vigorous on dull, calm days whilst on bright days with high wind it may be very reduced. For example, two *Metriocnemus* swarms, one in an exposed position and the other sheltered, were quite unaffected in size or vigour when cloud caused the light intensity to decline from 6000 to 850 f.c. (considerably above the level where light becomes limiting), but a sudden increase of wind rapidly dispersed the unsheltered swarm, which re-formed immediately the wind dropped, although the light intensity had not risen.

In species such as *Chironomus dorsalis*, with narrow limits of light toleration, light is undoubtedly a dominating factor governing the occurrence of swarming. Similarly at dawn, when the light is nearer the lower limit and wind is usually slight, illumination plays a very much larger part in the control of swarms of *S. minima* and *Metriocnemus*.

Observations suggest, however, that even when the light is well above the threshold for vigorous swarming a sudden burst of sunshine can stimulate resting flies to activity. Thus a sudden increase in intensity from 3000 to 6000 f.c. coincided with the appearance of large numbers of *Metriocnemus* which swarmed vigorously in the shelter of the inlet pipes, the wind remaining constant. Similarly a sudden increase in illumination can stimulate sluggish flies in the mating cage.

It has already been stated that each species swarms within a characteristic range of levels and that this is probably related to the increase in wind velocity with increasing altitude. Light intensity also increases with altitude and it seems likely that, within their characteristic range, positively phototropic species such as *S. minima* and *Metriocnemus* swarm as high as the increasing wind velocity will allow. The presence of sheltering objects tends to accentuate this response. In calm weather, therefore, *Metriocnemus* often swarms around the top of the Recorder House, where the light intensity is high, whilst, in the effluent pits, the greatest concentration of flies is at the top. On windy days, however, they are obliged to swarm nearer the ground in regions of lower light intensity. On one occasion a dense *Metriocnemus* swarm was noticed extending along the face of one of the channel walls, close to the top. The average light intensity in this situation was 4200 f.c. and the wind velocity 171 ft./min. The opposite wall of the channel, 5 ft. lower, was devoid of flies and here the light measured 3760 f.c. and the wind only 69 ft./min. Although the swarm along the upper wall was much disturbed by the wind, which twice dispersed it completely, the flies preferred this situation to the lower wall where conditions were calmer but the light intensity lower.

Thus it would appear that, within their characteristic zones, midge swarms are continually seeking a balance between optimum light intensity (maximum intensity in the case of *S. minima* and *Metriocnemus*) and the minimum shelter necessary for dancing. They fly, therefore, around the upper edges of sheltering

objects, but on calm days they spread into exposed positions taking advantage of all the light available until a rising wind drives them into shelter. Exceptions to this rule are, however, occasionally noted. Thus Ll. Lloyd (personal communication) describes small, dense, ball-like swarms of *Metriocnemus* in the open only 1 in. above patches of hemlock foliage, close to the ground, on a calm, very bright, sultry day.

(c) *Temperature.*

Temperature is well known to exercise an important influence on the flight of insects. Thus C. B. Williams (1940) has shown that the catch of insects in a light trap is doubled for an increase of 5° F. in minimum temperature or of 7° F. in maximum temperature. The effect of temperature on the mating dance does not appear to have been studied, although Cambournac and Hill (1940) suggest that, in company with relative humidity, it probably influences the time of swarming, whilst Rao and Russel (1938) state that no further swarms of *Anopheles annularis* were seen after the end of March, at which time the cool season ends.

No upper limit for the swarming of *S. minima* and *Metriocnemus* has been observed and it seems likely that they can dance vigorously in the highest temperatures encountered in this country. Both have been observed swarming in the sun when the shade temperatures ranged from 71° to 75° F. In the laboratory *S. minima* swarms actively in the mating cage when the temperature on the floor of the latter is 71° F., the temperature in the nucleus of the swarm, 1 in. below the lamps, being 10 to 20° F. higher.

Field observations, however, indicate the existence of a definite lower limit. During the course of 79 days' observations with *S. minima* no swarms have been noted when the temperature was below 46° F. Mating has twice been observed at 48° F. and twice at 50° F. The limits for *Metriocnemus longitarsus* are somewhat lower, as would be expected in a winter fly. Mating has been seen once at 47° F. and swarming without mating at 43° F. and 41° F. Once at 48° F. and once at 49° F. there were no signs of swarming, but these were days of very high wind velocity, sufficient to prevent swarming.

(d) *Humidity and precipitation.*

Various authors have suggested that relative humidity influences swarming. Cambournac and Hill (1940) found that in semi-enclosed pens *Anopheles maculipennis* var. *atroparvus* starts to swarm at a higher light intensity on evenings of moderate humidity than on dry evenings. Relative humidity is closely bound up with temperature and therefore difficult to analyse, but Williams (1940) has shown that night-flying insects exhibit a slight, but definite, tendency to select nights of high R.H. for increased activity.

No study of relative humidity has been undertaken in the present work. Certain field observations, however, suggest a wide range of humidity toleration for *S. minima* and *Metriocnemus*. Swarms of the latter have been observed at high altitudes on hot, dry days when the R.H. must have been low. On the other hand, swarming has been observed to take place during rain when the atmosphere must have been practically saturated. Ll. Lloyd (personal communication) records *S. minima* swarming and mating during a heavy shower which beat the individual insects down but did not stop the dance. *S. minima* has been seen swarming vigorously in all parts of the works in a thick fog. During observations at sunrise on 10.viii.41, when very vigorous swarming of *Metriocnemus*,

S. minima and *C. dorsalis* was in progress, heavy dew was noted on the glass covers of the instruments, indicating the saturation of the atmosphere. Furthermore, in some of the most favoured swarming haunts such as the effluent pits and certain channels (both of which are confined spaces generally containing water) and immediately above the wet surface of the beds the relative humidity must always be high.

5. The Orientation of Swarms.

(a) *Introduction.*

One of the most remarkable features of fly swarms is their manner of orientation over or near some conspicuous object. Many authors describe swarms orientated above tall trees, church towers, chimney pots, patches on the ground of some distinctive colour, etc. Moreover, the same situations are resorted to again and again by the same species (Hackett and Bates, 1936). Specially favoured situations at Knostrop have already been described (pp. 264–265).

Better understood is the so-called anemotactic response whereby the individual flies in a swarm orientate their bodies so as to face the wind. On the Knostrop beds where, near the ground, the prevailing wind is broken up by surface features into a number of separate air currents flowing in different directions it is possible to see neighbouring swarms facing different ways, but in each case the swarm is found to be orientated towards the air current of its locality and, whenever the direction of the latter changes, the orientation of the flies alters accordingly.

It is obvious that all hovering insects which form swarms should face the wind, for by flying against the stream of air and adjusting their own velocity to that of the breeze they keep stationary with respect to the ground below and gain buoyancy by utilising the force of the wind. Kennedy (1939) has shown that the mechanism of anemotaxis in hovering mosquitoes is entirely visual and that the insects so adjust their flight as to keep the images of objects on the ground stationary or moving only slowly with respect to their eyes. Whenever this becomes impossible the mosquitoes land. It seems highly probable that the mechanism of the anemotactic response in swarming Chironomidae operates in the same way. A tentative attempt to demonstrate this with *S. minima* on the lines of Kennedy's experiment was not successful, but further study is needed.

(*b*) *Theories concerning the mechanism of orientation.*

The orientation of swarming flies over raised objects, depressions and patches of contrasting colour is more complex and less well understood. Two main views have been advanced to account for them, viz.—

1. Radl (1904) contends that flies generally orientate themselves over an object because it stands out in some way from its surroundings. To support this view he cites cases of swarms, orientated over a raised object, moving away when another object is brought near, disorientated by its approach. He admits, however, that swarms occur with no apparent reference point.

2. Gruhl (1924) attributes aggregations of flies over high points to the special conditions of air-flow obtaining there. Air currents pass over small obstacles in an undulating manner, the ascending current forming a corresponding descending stream. Insects will therefore find at high points the

appropriate requirements for flight. In strong winds they dance in the shelter of the obstacle, for the calmest region is behind the barrier.

On the other hand, Cambournac and Hill (1940) regularly observed swarms of *Anopheles maculipennis* over the corners of buildings, the eaves of houses, paths, etc., or simply over the ground without any special reference to objects below and could discover no factors influencing the choice of position except proximity to the daytime shelters and protection from the wind.

Present observations and experiments suggest that none of these views can alone account for all cases of orientation, but probably all these factors, singly or in combination, are acting at different times. Howard, Dyar and Knab (1912) considered that both air currents and light influenced the position of swarms and suggested that flies orientating over spots on the ground belonged to different species from those over raised objects, but this seems highly improbable.

(c) *Orientation to air currents.*

Certain commonly observed orientations at Knostrop seem to be conditioned, wholly or mainly, by local air currents. Thus in the westernmost of the concrete channels the physical conditions are such that, except when the wind is blowing parallel with the channel, the air currents (determined by observing the drift of *Lycopodium* powder) are always very constant. The current is reflected from the longitudinal walls and divides, one stream flowing towards the north end and the other to the south. In the channel ends the stream rises and flows vertically up the end walls (8 ft. high) and passes out to mingle with the general wind current. These channel ends are more frequently resorted to by swarming *S. minima* and *Metriocnemus* than any other part of the works and swarms are frequently seen there when the rest of the channel is devoid of flies. The flies in the channel thus show a preference for the regions of rising air currents, but these positions are also regions of maximum shelter, for anemometer tests show the air velocity to be considerably checked in the channel ends.

In the effluent pits the air currents are more complicated, but tests showed that two regions occurred where horizontal wind velocity was at a minimum. These were—(i) just to the east of a horizontal partition wall where two opposing currents neutralise each other and result in a region of practically still air, and (ii) over a central manhole which marks the centre of a slowly rising and swirling current. It is these two points which are most favoured by *Metriocnemus* swarms. It was thought possible that the flies over the manhole were orientated to the black colour of the latter or to the light reflected from the water it contained, but when sheets of black or white paper were placed over the mouth of the manhole the swarm dispersed. If the orientation had been conditioned solely by the black colour of the manhole the black paper would not have dispersed the flies, nor would the white paper if they had been orientated to the reflected light. The paper, however, cut off the ascending air stream and it seems likely that this was responsible for the orientation of the swarm. Black or white papers placed alongside the manhole failed to alter the disposition of the swarm.

Manholes, 2 ft. 6 in. square and about 7 ft. deep, occur at either end of the beds and pairs of manholes are connected by subterranean tunnels running beneath the beds. The manholes are covered by gratings and these are much favoured by *Metriocnemus* and *S. minima* which may often be seen dancing

over the bars in the shelter of the manhole covers. When the wind is blowing from the south, tests showed that air enters the southern manholes causing a down-draught and, passing beneath the beds, emerges through the northern manholes, and vice versa. A strong down-draught is sufficient to prevent all swarming. At the other end of the beds, where the air stream is emerging from the manholes, a strong up-draught is correlated with the absence of *S. minima* from the gratings, although it may often be seen swarming vigorously alongside them. *Metriocnemus*, on the other hand, appears to favour manholes from which a stream of air is rising and when one of these was wholly or partially covered with black paper the flies were repelled from the covered area, which was then invaded by *S. minima*. Similar results were obtained with white paper, ruling out light reflected from the water at the bottom of the manhole as the conditioning factor. The temperature difference between the grating and the adjacent ground was only 0·5° F., and was therefore negligible. *S. minima* will swarm over manholes from which only a gentle draught is rising.

The vertical air currents dealt with above were all of the nature of draughts, but many authors have suggested that convection currents may be important (Marshall, 1938). In experiments in which swarms in glass cylinders through which convection currents were rising were compared with others in control cylinders no difference in readiness to swarm or other behaviour was noted, nor did the flies in a cylinder orientate over a small movable glass cell through which warm water was circulating. Although the experiments failed to demonstrate any response to convection currents they are not conclusive, but it is likely that orientation under natural conditions is more often due to the influence of vertical currents produced by the wind flowing over irregular surfaces than by convection.

Swarming can occur in perfectly still air with convection currents completely eliminated, for a good dance of *S. minima* was obtained in a closed cylinder, surrounded by a larger cylinder to exclude draughts and with a cell of copper sulphate solution interposed between the overhead lamp and the top of the cylinder to eliminate heat rays.

Thus, while field observations suggest that flies tend to orientate in gently rising currents, swarming is equally vigorous in perfectly still air and it would appear that they seek regions of rising air because these are also regions where the adverse effects of horizontal currents are at a minimum.

(d) *Orientation to light.*

i. Field observations.

There exist, however, certain orientations for which light appears to be the chief conditioning factor. Cases are reported where two swarms of the same species, dancing at the same time, showed a preference for different light intensities. Thus, Cambournac and Hill (1940) describe a swarm of *Anopheles maculipennis* near the window of a stable and another in a dark region in the centre of a barn. In addition to the *Metriocnemus* swarm over the manhole of an effluent pit (p. 280) a second is sometimes seen immediately above the first and nearer the top of the pit in a region of higher light intensity. If this latter, more exposed, swarm is beaten down by the wind it does not join the lower swarm but the flies settle, only to re-form as before as soon as the wind allows. *Metriocnemus*, swarming near the top of the Recorder House, forms aggregations of flies at the corners of the building on its lee side and these may be joined by a horizontal band of flies which, in calm weather, has the form of a bow.

Measurements made in various parts of the swarm showed the band to be following a line of equal light intensity.

Clear cases of the importance of light are afforded by a study of the orientation of swarms in relation to background. Dense swarms of *Metriocnemus* are sometimes seen extending along the top of the bed wall of the western concrete channel. A sheet of white paper, 3 ft. long, was draped over the top of the wall so that about 20 in. hung down its vertical face. Immediately the flies in front of the paper were repelled so that the swarm opposite the paper took on the form of a horizontal bow with aggregations opposite the ends of the sheet. A similar sheet of black paper, 4 yd. away from the white, attracted flies towards it so that the swarm in its vicinity became denser than that along the adjacent parts of the wall. Brown paper had no effect on the swarm. In one experiment the intensities of the reflected light, measured 2 in. in front of the paper and wall were as follows—white 500 f.c., brown 250 f.c., black 80 f.c., wall 150 f.c. The distance at which the flies swarmed from the background thus seemed to be directly related to the intensity of reflected light, although measurements in the bow of flies in front of the white paper showed the flies to be following no fixed line of light intensity.

A related phenomenon was observed in a small *S. minima* swarm dancing in the shelter of a grass bank at the north end of the same channel. The base of the swarm was about 1 ft. above the ground. When a piece of white paper was placed on the ground beneath the swarm the flies at first dispersed (disturbed by the action of inserting the paper) but rapidly re-formed about 5 in. higher. When the paper was removed the swarm re-formed at its original level. With black paper the swarm, on re-forming, retained its original height.

ii. Laboratory experiments with coloured backgrounds.

In order to investigate the effect of background more fully, experiments were performed under controlled conditions in the laboratory. A standard method was adopted. A good swarm of *S. minima* was induced in the mating cage which was lighted from above by two 40-watt lamps. Each lamp throws a cone of light into the cage. At the top of the latter the regions of highest intensity are situated immediately below each lamp (290 f.c.) whilst on the floor, where the cones overlap, the region of highest intensity is in the centre (45 f.c.). In a preliminary test, using smooth white cardboard on one half of the floor and matt surface black paper on the other, the intensity of reflected light 1 in. from the floor of the cage was 1 f.c. over the black and 8·5 f.c. over the white. At the top of the cage the reflected light was approximately equal, being 4 f.c. on both sides. These lighting conditions were kept constant throughout the experiments, which were performed in a darkened room.

With the floor of the cage uniformly white the swarm was evenly distributed, but when a sheet of black paper was slipped over the left half of the floor the flies instantly migrated to the right and continued to swarm over the white cardboard. When the black paper was removed and placed over the right half the flies immediately moved to the left, so that they were once more over the white. When the black paper was placed in the centre of the floor, leaving a strip of white cardboard at either end, the swarm divided and about half the flies danced over each of the exposed white areas. When the black paper was moved slowly across the floor, from left to right, the flies crowded more and more into the right portion, but with the paper half-way across the flies began to leave the right side and cross the black paper towards the left, where they

continued to dance over the white strip. More and more flies crossed the paper as it approached the right-hand end, until the bulk of them were swarming over the white cardboard on the left and only a small residual swarm was left over the black paper. The residual swarm does not appear to be any larger when the paper is advanced slowly across the floor rather than suddenly.

Experiments were then performed with papers of the following colours— light red, dark red, light blue, dark blue, green, yellow and dark purple. These were used in pairs in various combinations and in combination with black and white. The results showed that :—

1. White is preferred to all colours except yellow.
2. Light colours are preferred to dark, even when they are shades of the same colour.
3. The response to two strongly contrasting shades, such as yellow and purple or black and white, is complete and rapid, whereas that to two colours of less marked contrast (*e.g.* yellow and green, light blue and white) is slower and sometimes less stable.
4. Where the colours are of approximately similar tone, such as yellow and white, dark red and dark blue or purple and black, the flies show no marked preference.
5. The repulsion of the flies by an unfavourable colour is not merely due to the mechanical action of inserting the paper, since it does not occur when a sheet of white paper is inserted over an all-white background.
6. Not only does the colour of the background affect the density of the swarm above it, but it also determines the height at which swarming takes place, the swarm being higher over light colours than over dark.

These observations suggest that it is the quantity of light (intensity) rather than the quality (colour) which is the important factor and to test the accuracy of this conclusion the following experiments were performed :— (*a*) Black paper was placed over the left half of the floor of the cage, the right half being white. The right-hand lamp was removed and the left tilted so that no direct light was thrown on to the white cardboard. The swarm moved rapidly to the left side and danced over the black paper, thus showing a preference for the more strongly illuminated background even though it was of apparently unfavourable colour. (*b*) The colour contrast was replaced by a contrast between reflecting and non-reflecting surfaces. The floor was completely covered with matt black paper and the various reflecting surfaces were placed on one side of the floor. A sheet of glass, a circular mirror and a petri dish filled with water were used in turn and in all cases the swarm showed a definite attraction to the side on which the reflector was placed, although the response was never so rapid or clear as with surfaces of strongly contrasting colour. It is not possible, however, to separate the effects of reflection entirely from colour difference, for in all cases the yellow image of the lamp is strongly mirrored in the reflecting surface.

This preference of *S. minima* swarms for the lightest backgrounds may be merely a corollary of the natural positive phototropism of the species but it is obvious that the rising females will be more conspicuous against a light area.

Cambournac and Hill (1940) record that a swarm of *Anopheles maculipennis* in a barn concentrated over a sheet of white paper 30 × 30 cm., placed on the floor. If the paper was removed the swarm spread out to cover an area 80 × 80 cm. It is obvious that if the reflecting area be made very small the amount of light reflected from it may not be sufficiently great to attract the flies. Moreover, a large swarm may not be able to concentrate over it from purely spatial

considerations. Using a black background in the mating cage of total area 1128 sq. cm., squares of white paper of various sizes were placed in the centre of one half of the floor of the cage. With a swarm of several hundred flies, no tendency to orientate over the half containing the white paper was observed when the area of the latter was less than 25 sq. cm., but definite orientation occurred with areas above this.

(e) *Orientation with respect to raised objects.*

Whilst the orientations described above can be attributed wholly or mainly to air currents or to visual stimuli, the mechanism of the orientation of fly swarms in relation to raised objects or depressions is more difficult to analyse. This feature of fly swarming is the most frequently mentioned in the literature (*e.g.* Howard, Dyar and Knab, 1912; Edwards, 1929; Rao and Russel, 1938; Marshall, 1938).

i. Orientation to special air conditions.

Some of these orientations may be due merely to the desire of the flies to obtain shelter from the wind, as in the case of the swarms of *Culex pipiens* on the lee side or corn stooks described by Howard, Dyar and Knab. In calm weather such swarms fly above the reference object, but in a strong breeze they are found on the lee side, a little below the top.

Flies are frequently seen swarming over depressions in the ground which afford shelter, but since these frequently harbour water the additional complication of the attractive effect of the latter is introduced. *S. minima* has often been seen swarming in damp pits and channels at Knostrop and avoiding dry ones nearby. Water may well exert an attractive effect on the flies, for as well as usually being at a lower level than its surroundings, it reflects more light. Moreover the majority of swarming Diptera oviposit in water.

The relative value of colour contrast and shelter was investigated in the case of small swarms of *S. minima* and *Metriocnemus* seen over a grass bank at Knostrop. Each swarm was orientated over a patch of contrasting ground colour, produced by small heaps of light brown debris scattered among the long grass. These heaps not only contrasted in colour with the grass, but formed sheltered depressions. A strong breeze was blowing and the flies kept almost entirely below the level of the top of the grass. The bottoms of some of the depressions were covered with freshly picked grass to destroy the colour contrast. The swarms were unaffected. The grass was then trodden down for two or three feet on the windward side of each depression, allowing the breeze to enter. The swarms dispersed or, in one case, advanced to the forward boundary of the enlarged depression and danced there. On raising the grass this swarm retired to its original position whilst those that had dispersed reformed. These observations suggest that, in this case, shelter was the main factor determining orientation over the coloured patches.

Swarms of *S. minima* and *Metriocnemus* have frequently been seen orientated over small objects on the ground. Such objects might conceivably set up favourable air currents or the orientation might be entirely visual. *S. minima* orientating over glass jars, a grey attache case and a pair of red rubber gloves was unaffected by the removal of these objects, but it must be remembered that such objects always cause depressions in the grass which are left behind when they are removed and may therefore give some degree of shelter.

ii. Orientation to visual stimuli.

The high-flying swarms of *C. dorsalis* afford many instances of orientation in which shelter cannot possibly play any part, since the swarms often occur too far above the ground to derive any direct protection from surface features. Five such swarms were seen in a lane, 5–10 ft. above the ground. Three were flying above three small heaps of white stone by the roadside, whilst the other two were over a hedge, but the actual points of the latter over which they were swarming were not marked out in any way from the rest. Similarly the large aggregations seen round the ends of the concrete channels are usually too high to obtain any direct shelter from the sewage conduits or other ground features. Often a swarm may be seen many feet above the top of one of the channel walls taking the form of a narrow band in conformity with the shape of the wall.

In such cases the swarms may benefit by vertical air currents set up by the objects above which they are orientating, but this cannot account for swarms scattered at various points high over the beds and paths. Over the beds any rising current set up by the warm sewage would have been completely obliterated by the breeze at the height at which the dances were occurring and in no case could any orientation mark be found on the ground below them. One such swarm had its base about 15 ft. above the surface of the bed and was columnar in shape and at least 4 ft. in diameter but, when the observer walked beneath, it contracted to a narrow column, 18–24 in. wide, above his head. On walking away rapidly, it expanded to its original size and the response was so rapid that it is difficult to suppose it to have been due to air currents set up by the observer's body. In this case it would seem that the stimulus can only have been visual.

iii. Swarming over the tallest object.

A striking feature concerning orientation over raised objects is the manner in which, in calm weather, flies always choose to swarm over the highest feature available. Gruhl (1924) describes how a swarm of *Culex nemorosus*, over a fir tree 2·5 m. high, could be dislodged by raising a net over his head, when the swarm gathered over the top of the net. Knab (Howard, Dyar and Knab, 1912) relates that *Culex pipiens* which had gathered over the heads of persons entering the field in which it was swarming could be got rid of only by passing under some taller object, above which the swarm would remain. At Knostrop, on calm days, *Metriocnemus* swarms around the tallest features, such as the superstructure of the distributors and the top of the Recorder House.

Since high objects are, as a rule, more brightly illuminated than low ones, it may be that this preference is the result of a light-wind relationship (see pp. 277–278), the flies choosing the most highly illuminated position that affords the requisite amount of shelter.

iv. Indoor swarming.

When swarming occurs indoors there is usually little wind to account for the orientations, although slight air currents may be present. Yet marked preferences for particular positions are exhibited and the same positions are always resorted to, even by different batches of flies. Rao and Russel (1938) describe swarms of this type in various culicines.

When a trap of *S. minima* was released freely into the laboratory the swarms always formed in definite positions. Some always occurred below a suspended wall lamp, when this was alight, where bright overhead illumination and a

convection current were to be found. Others usually made for the edge of the windowsill or the corner of a table close to the window.

About 1000 flies were released into a laboratory, lighted along one side by two high windows. A bench, 3 ft. wide, runs the full length of the room in front of the windows and a swarm of about 50 flies soon formed at the edge of it in front of the left-hand window, open to the sky, whilst a swarm of about 20 flies was found in a similar position in front of the right-hand window, which faces a higher brick building 10 yd. away. The bench is slightly forward of the window ledge so that light strikes directly on to the floor below the bench. Tests showed gentle upward air currents in the positions of the swarms. 75 minutes later the right-hand swarm had disappeared. A box, 18 × 12 in., was placed on the bench in front of the left-hand window, screening the flies in this region from the light. The swarm immediately shifted to the right of the box. As the latter was pushed slowly along the bench, from left to right, the swarm kept always ahead of it until it came in front of the wall separating the two windows, where the direct light is cut off. Here the swarm dispersed, but re-formed in front of the right-hand window. Subsequently a swarm reappeared in front of the left-hand window. It would therefore seem that light was largely conditioning this orientation. Although the light enters laterally, the flies, by keeping just below the top of the bench, are illuminated mainly from above, as in the mating cage. The lateral phototropic response is not invoked and swarming takes place. In two other areas of the laboratory, where swarms habitually formed, gentle upward currents, conditioned by the disposition of the furniture, were noted.

v. Laboratory experiments with raised objects.

The orientation of *S. minima* swarms with respect to raised objects was studied under controlled conditions in the mating cage, using the same standard conditions of lighting as in the experiments with coloured backgrounds (p. 282).

A. Orientation in still air.

The floor of the cage was covered with matt black paper. Flies were released into the cage and a large swarm obtained. Two cylindrical tins, 4 in. high and 2·4 in. in diameter, one covered with matt black paper and the other with white, were used as orientation objects.

With no objects in the cage the swarm remained evenly distributed, the flies swarming low over the black background. When a white cylinder was placed in the centre of the cage the swarm showed a distinct tendency to aggregate over the top of it, but resumed its original distribution as soon as the cylinder was removed. There was, however, no aggregation over the black cylinder when this was substituted for the white. A choice of colour was then provided by placing the white object in the centre of one half of the cage and the black in the centre of the other half. Aggregation of flies 1·5–2 in. above the top of the white cylinder was noted but no aggregation over the black, the flies swarming low over the top of the latter. When the black background was replaced by white no orientation over either cylinder was seen.

B. Orientation in wind.

An electric fan, working through a rheostat, was used to provide a current of air through the cage, from right to left as in the experiments on wind velocity (p. 272). It should be noted that the bolting silk covering the left-hand end of the

cage reflects a good deal of the stream of air, setting up eddy currents which reach regions of the cage which would otherwise be sheltered by the cylinder, and so to some extent destroys its sheltering effect. This reflected current becomes particularly important when the cylinder is placed near the left-hand end.

Using a white cylinder centrally placed on a white background, the flies remained evenly distributed, showing no orientation to the cylinder as long as no wind was passing, but with gradually increasing wind velocity the swarm became progressively divided into two portions over the leeward and windward edges of the cylinder. Eventually most of the flies in the cage were put down except the two swarms in these positions. At higher velocities the windward swarm was dispersed, but that on the lee side of the cylinder remained, though somewhat forced back from its original position. The swarm could be retained in this situation by occasionally reducing the wind velocity, allowing the flies to recover whenever they showed signs of exhaustion. This process simulates the behaviour of a gusty wind and is no doubt the mechanism which holds chironomid swarms above and behind trees, etc. Identical results were obtained with a black cylinder.

When a black background was substituted for white, essentially similar results were obtained, the final swarm being orientated over the leeward edge of both black and white cylinders when a breeze was passing.

Two main conclusions may be drawn from these experiments :—

1. In still air, *S. minima* orientates over a cylinder only if it is attractively coloured with respect to the background (*e.g.* white on black). Swarms do not orientate over a white cylinder standing on an equally attractive white background, nor will they orientate over a cylinder of unattractive colour, even if it contrasts strongly with the background (*e.g.* black on white).

2. In a strong breeze the flies remaining in the air are always orientated over or near the cylinder whatever its colour or that of the background so that, in the main, wind has masked the light response.

Light, however, still seems to exert some effect, for in a second series of experiments in which the cylinder was placed near one end of the cage, instead of centrally, it was found that when the cylinder was near the left-hand end the remaining swarm, instead of being to the lee of the cylinder, was immediately above it or slightly to the windward side. It thus inclined to the region of highest illumination in the cage, but it is possible that currents reflected from the end of the cage might be playing some part.

To study the effect of shelter a white cardboard partition, 8 in. high and 9·4 in. wide, was fixed vertically across the cage, fitting tightly against the glass on either side. When a current of air was passed a test with *Lycopodium* powder showed that some air flowed out of the cage on the lee side of the partition through the bolting silk covering the left-hand end, whilst some was reflected by the bolting silk forming a powerful eddy current. Owing to the large quantity of air so reflected, this eddy current was relatively far stronger than normal eddies occurring on the lee side of objects in nature and, to this extent, the conditions in the cage were artificial.

In still air the flies were distributed equally on both sides of the partition. When a gentle breeze was passed those flies above the partition (unsheltered) sank below the top or settled on the sides of the cage. As the wind force was gradually increased both swarms were reduced in size, the lee less than the windward, until finally the windward swarm dispersed entirely, leaving a small swarm on the lee of the obstacle. At the highest velocities the lee swarm may

also be put down. The flies on the windward side of the wall faced to the right (towards the wind), those on the lee side towards the left (*i.e.* towards the reflected current).

Similar results were obtained when the partition was placed in the centre of the right-hand half of the cage, except that the main aggregation of the lee-side swarm is not near the partition, but under the left-hand lamp which, under these conditions, is a region of maximum illumination in the cage.

When a partition was placed near the left-hand end of the cage the *lee* swarm was eliminated before the windward. This was probably due to the powerful reflected current and, though this could not have been stronger than the direct wind on the right of the partition, its strong swirling motion may be more powerful to prevent flight than a horizontal current. Furthermore, the space between the partition and the left-hand end of the cage was small and contained few flies, so that the swarm was never so large or vigorous as that on the right of the partition and, hence, more easily put down.

The substitution of a black background for the white made no difference to these responses, except that all the swarms flew lower. Flies never showed any tendency to form aggregations over the top of the white partition except when this was on a black background and immediately below one of the lamps, thus coinciding with the most strongly illuminated region of the cage.

This experiment demonstrates that both the windward and lee sides of a wall afford shelter from a wind at right angles to it, the former by virtue of the rising current set up which partly counteracts the effect of the horizontal current, whilst the lee side is sheltered entirely from the horizontal wind, but is exposed to eddies set up behind the wall. Flies swarming on the lee of an obstacle are the most protected, but those swarming on its windward side or even directly above it obtain some degree of protection.

Flies swarming above the top of an obstacle are blown across to the lee side, settle there and rise to swarm on that side during the next calm. Thus flies accumulate on the lee of an obstacle. This process was seen regularly in the mating cage during the above experiments and may be, in part, the mechanism that causes swarming to the lee of barriers in nature, the flies being carried there by the wind and not deliberately seeking out sheltered situations.

vi. Adherent swarms.

Fly swarms have frequently been observed to accompany a moving person or object (Radl, 1904; Cambournac and Hill, 1940). On still days at Knostrop swarms of *Metriocnemus* and *S. minima* can frequently be seen travelling above or in front of the sewage distributors as they traverse the beds. *Metriocnemus* prefers the higher parts of the machines, whilst *S. minima* commonly orientates itself along the horizontal arms, a few inches above the bed surface.

In some cases following swarms are clearly seeking shelter from the wind. On one occasion the author, while riding a bicycle, was followed by a very large and dense *Metriocnemus* swarm which kept to the lee side through every turn and never rose above shoulder level. Similarly a dense swarm of *Metriocnemus* and *S. minima* moved round to the author's lee side when he approached it and followed him as he walked slowly towards a similar swarm some 40 yd. distant. Each time the wind rose the flies sank to the ground to rise and re-form in their original position as soon as the wind fell. Once, when the wind veered from S.E. to N.E., the swarm moved through 90° to come again on to the lee side. By walking slowly the flies could be transferred from the shelter of the sewage

conduit of one bed to that of the next, but many were lost on the way and on arrival the swarm was less than half its original size. On returning a new and equally large swarm had formed in the original position of the former one. This transfer was repeated three times, but in a fourth attempt the swarm was completely lost before it had been taken half-way across.

In other cases, however, it seems impossible that shelter can be responsible for the reaction. When a swarm forms low over the head of a person it may be readily supposed to be deriving some benefit from the disturbance of the air currents caused by his body, but it is difficult to see how this can apply when the swarm is many feet above his head. Thus the swarm of *C. dorsalis* referred to on p. 285 not only contracted as the author passed beneath, but actually followed his slow walk, although its base was at least 9 ft. above his head, becoming stationary whenever his pace increased. It was undisturbed by the distributor passing below, but a similar swarm over another part of the bed followed high over the arm of a distributor. In such cases the swarm probably uses the object as a visual orientation mark and travels with it in order to keep its image stationary with respect to the insects.

(f) *Conclusions.*

A general statement of the conclusions upon orientation may now be attempted.

1. There are two main types of orientation, viz.—(*a*) directional orientation of the individual flies towards the wind (anemotaxis), and (*b*) orientation of the whole swarm with respect to some reference point. The former is the necessary outcome of the means by which flies counteract the air currents, and Kennedy has shown that it is conditioned by a visual response to moving images.

2. In orientation with respect to a reference point reactions both to light and air currents occur, thus combining, in part, the views of Gruhl and Radl. Orientations due to either factor separately are rare in nature, although they have been produced in the laboratory. In the open air wind is usually the dominant factor.

3. An example of pure light orientation is afforded by the reaction of swarms to coloured backgrounds. With *S. minima* it seems that it is not the colour but the total quantity of light, direct and reflected, that is important, the flies choosing the region of greatest illumination. *Metriocnemus*, which in general chooses elevated situations of high light intensity, appears to concentrate over black paper. Moreover, both *Metriocnemus* and *S. minima* fly closer to a black surface than a white. These reactions are, as yet, imperfectly understood, but the greater visibility of the females against light areas is probably important.

4. In completely still air flies orientate over a raised object in the mating cage only if it reflects considerably more light than the background.

5. With respect to air currents, those regions tend to be favoured where the main force of the wind is disturbed by counter currents so that calmer patches result. Such currents may be set up by convection, depressions in the ground or by a raised object. Rising currents, when they are not too strong, are favoured by all species. The regions to windward and to lee of a raised object, by simple shielding or by virtue of the counter currents set up are more sheltered than the region immediately above it, but the lee side is the more protected of the two.

6. Laboratory experiments show that the aggregation of flies behind or above an object can be enforced by the wind by purely mechanical means and

the flies need not deliberately seek sheltered areas. A swarm can be held in a favourable position (*e.g.* above or behind a cylinder) by a rapidly varying air current.

7. The choice of a position is probably a compromise between the desire to obtain optimum light intensity (*i.e.*, maximum intensity in the diurnal swarming *S. minima* and *Metriocnemus*) and the necessity for gaining sufficient shelter from the wind. Thus, in light breezes, flies usually swarm above their reference objects and, in strong winds, behind them. When a swarm, adherent to a moving object, passes below a higher one giving the necessary amount of shelter, it may attach itself to the latter in order to obtain more light.

8. In many cases swarms probably adhere to moving objects because of the shelter or favourable air currents derived from them. When they are too high above an object to admit of this possibility, the reaction may perhaps be explained as an attempt to keep the image of the latter stationary.

6. Discussion: The Biological Significance of the Mating Swarm.

According to Gruhl (1927), the mating swarm possesses three main characteristics which distinguish it from other assemblies of flying insects. These are—(i) the insects hover in a defined place in the air, (ii) through the hovering movements the air currents are mastered in a varied, but highly characteristic, fashion by which the impression of dancing is given, (iii) the dance leads to mating. Although in the present work reference has only been made to the Chironomidae and Culicidae, true swarming occurs among the Empidae and Tipulidae and in certain groups outside the Diptera. Gruhl has examined the dances of Ephemeroptera, Trichoptera and the lepidopteran *Adela* and concludes that they fulfil all the requirements of a mating dance.

Certain characteristic features are possessed by swarming insects. All are lightly built (swarming does not occur in the characteristically heavy-bodied orders such as the Coleoptera and the Hemiptera) and possess strong powers of flight. Many male flies have greatly enlarged eyes due, according to Gruhl, to the wide outlook afforded by the lofty height at which they dance. This feature is shared by mayflies and by certain Hymenoptera which exhibit a hovering flight and is always associated with the habit of "marriage by capture" (Richards, 1927). There appear, however, to be no structural peculiarities of the wings associated with swarming. The capacity to hover in one place, which is essential for the full development of the swarm, occurs sporadically throughout the Diptera and is also found in many forms which have not developed the habit of swarming.

Since swarming is usually the prelude to mating it is natural to suppose that it facilitates the latter in some manner. Perez, quoted by Gruhl (1924), held that the dance had the purpose of bringing the sexes together and that, in the Diptera, the males await the females and do not seek them. Gruhl, however, notes that this is not entirely true, for in many species (*e.g.* in the Dolichopodidae, Empidae and Syrphidae) the males do the seeking. Howard, Dyar and Knab (1912) thought that the swarm appeared attractive to the female.

In widely roaming species, like most of the Diptera, the chances of single males and females meeting would not seem to be very great. If, however, the males form aggregations near the haunts of the females they may form a body sufficiently large to be perceptible to the females either by sight or sound (a large swarm emits a loud hum, readily audible to the human ear) which they

would most certainly join to effect mating. Conversely, the females may form a swarm to which the males resort.

More difficult to understand are those cases where swarming does not lead directly to copulation, as in *Aporomyia dubia* where the males dance before the females appear and *Culex fatigans* where the sexes dance separately (Gruhl, 1924). In other species mating may occur without a swarm. Thus Marshall (1938) relates that at the Malaria Control Institute, Hayling, *Culex molestus* has been bred for some years in glass incubators the size of a jam pot. Although unable to indulge in swarming, the flies may perhaps desire to do so and often manifest increased activity at dusk by very audible buzzing. *Metriocnemus longitarsus* can also dispense with the swarm if necessary and mate in the confined spaces in the beds which is of great advantage to a fly active in winter when long periods of wind prevent the formation of swarms (Lloyd *et al.*, 1940).

An interesting transitional state is found in *Anopheles maculipennis* var. *atroparvus* (Cambournac and Hill, 1940). In enclosed pens mating begins on the walls, but is soon followed by swarming of some of the males. The outdoor swarms which begin later are not resorted to by the females as frequently as would be expected if the swarms were exclusively for mating and the authors suggest that since many, perhaps most, of the females are fecundated inside the shelters it is possible that the dance has largely lost its functional character, although the form of the ritual is preserved.

In such cases the dance cannot assist one sex to find the other. It is, however, possible that swarming is a form of mass stimulation, either through sight or sound, which brings the swarmers into the correct physiological state for mating. Such cases are common in other animals, especially birds where the rituals of courtship have a definite stimulating function on both sexes designed to bring about the synchronisation of sexual receptivity. Again it is possible that the dance may play a part in the maturation of the gonads. Uvarov (1928) has shown that the gonads of the migratory locust are not mature until after the migration flight, and that the resultant increase in body temperature induces this maturation. In swarming Diptera flight often lasts for so short a time before copulation that it could not possibly have any influence on the ripening of the gonads, but conceivably might facilitate the release of the sperm. This idea was tested in the following experiment.

A laboratory culture of about 200 *S. minima* which had not previously swarmed was released into the mating cage under the usual conditions. From the resulting swarm the following specimens were taken for examination: (i) 7 males which settled immediately and were captured before they could take any part in the swarm, (ii) 10 single males, captured as they fell out of the swarm to rest; the last was taken 30 mins. after swarming had commenced and may possibly have copulated, (iii) 10 copulating pairs. Each male was kept alive in a separate glass tube until required, when it was lightly anaesthetised with ether and the reproductive organs, which are similar to those described by Miall and Hammond (1900) for *Chironomus*, dissected out and examined in saline solution under the microscope. Sperm was observed in the testes, vasa deferentia and vesiculae seminales of all specimens and in the proximal end of the ductus ejaculatoris of one of the swarming and one of the non-swarming males. Sperm was noted in the distal end of the ductus in two males which had copulated and in one of these peristalsis was still proceeding, driving sperm down the ducts.

Thus there was no general difference in the distribution of sperm in relation to swarming, and some of the flies which had copulated were similar to those

which had not done so. Further, no difference could be detected in the state of the reproductive organs between the three groups. The evidence therefore suggests that no visible changes in the reproductive organs take place during the mating dance. In any case, as the males often copulate immediately on entry to the swarm, and so before dancing, it is very unlikely that any conditioning change in the reproductive system occurs. Some form of nervous or hormonic change which could be rapidly induced by the dance would seem to be more likely.

If dancing were responsible for some physiological change in the flies it renders understandable those cases where mating occurs some time after swarming has ended. However, many species closely allied to the swarmers dispense with the dance whilst others can mate with or without it, as in the genus *Aedes*, where *A. communis* and other species swarm regularly, whilst *A. atropalpus* appears never to do so. Swarming, therefore, would not seem to be essential for mating but merely facilitates and prepares for it, perhaps simply by providing a conspicuous collection of one sex to which the other can resort with the certainty of effecting copulation. Changes of habit, such as the frequenting of small enclosures by large numbers of the same species, may render the swarm unnecessary and in these cases the dance may become divorced from the actual mating as a prelude to its total suppression.

It might be considered that aggregations of swarming insects would be very vulnerable to the attacks of predators, but Gruhl (1927) has shown that, contrary to expectation, the swarmers enjoy a high degree of immunity. This fact, he argues, would act as a sustaining principle, tending to fix the habit once it had been acquired.

The problem of swarming in insects is both complex and obscure and has received little scientific investigation in the past. Yet the subject is one of practical importance since many of the swarmers are the vectors of disease and a full understanding of their breeding habits is necessary both for the control of the insect in its natural haunts and for the maintenance of laboratory cultures for experimentation. The reactions of swarms to raised objects and to various conditions of wind and light form an interesting and complex study in animal behaviour whilst in the mating dance is seen the beginnings of social behaviour in otherwise solitary species. The whole topic, therefore, deserves more attention than it has hitherto received and requires a more complete and thorough investigation, particularly along experimental lines, than has been possible in this work. Such studies should necessarily be preceded by a detailed examination of the sensory physiology and behaviour of the species concerned.

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7. Summary.

The swarming habits of chironomids common about sewage works are examined with experimental evidence and comparisons are drawn with the recorded facts about culicines. *Spaniotoma minima* and *Metriocnemus* spp. are diurnal swarmers while *Chironomus dorsalis* is crepuscular. Each has a

characteristic altitude zone based on the ground or on some raised object and proportional to the size of the fly. Within this limited zone each of the diurnal swarmers seeks maximum light and therefore swarms at the greatest height permitted by the wind. Discrete swarms are thus the result of a conflict between these factors. Background has some influence on choice of site, probably due to the fact that the females are more conspicuous against lighter colours or reflecting surfaces and partly to the phototropic behaviour of the species. The lower limits of temperature and of light tolerance are defined approximately and the upper limit of air current. There is no lower limit for air current and with the diurnal swarmers no upper limit for temperature or light appeared. The greatest range of air humidity does not inhibit dancing in the diurnal-swarming species. The purpose of the swarm is considered and the conclusion drawn that it leads to more easy meeting of the sexes through vision or possibly sound. It does not lead to any evident conditioning of the males, since no apparent change in the reproductive organs or movement of sperm results. There may be a mass stimulatory effect. *S. minima* will not swarm in small containers if the light is dominantly unilateral, but will do so with uniform lateral light or with dominant light from below. Vigorous swarms with free and effective mating are, however, most readily gained by dominant lighting from above. Under the last conditions *S. minima* can be bred readily in captivity.

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